ISORTHIS AND *SALOPINA* (BRACHIOPODA) IN THE LUDLOVIAN OF THE WELSH BORDERLAND

by VICTOR G. WALMSLEY

ABSTRACT. Examination of the enteletacean brachiopod members of the faunal assemblages now used in British Ludlovian stratigraphy (Holland, Lawson, and Walmsley 1963) and comparison with a large collection of Silurian and Lower Devonian brachiopods from many parts of the world, reveals that the species commonly determined as *Dalmanella lunata* (J. de C. Sowerby) and *D. orbicularis* (J. de C. Sowerby), have not yet been found, (though sometimes recorded), from areas outside Britain. However, one of the new species of *Isorthis* here described has a wide distribution in Britain and occurs in North America (Maine and New Brunswick) and South America (Venezuela). *Salopina* Boucot is emended and *Salopina lunata* is described, figured and distinguished from *S. submedia* (McLearn), which was figured as *S. lunata* by Boucot 1960, from New Brunswick. *Isorthis* Kozlowski is emended and *Orthis orbicularis* J. de C. Sowerby together with two new species (*I. amplificata* and *I. clivosa*), and two new subspecies (*I. scuteformis scuteformis* and *I. scuteformis uskensis*), from the Welsh Borderland and a new, related species (*I. slitensis*) from Gotland, are assigned to *Isorthis* and described and figured.

IN order that the refinements of stratigraphy and correlation recently achieved in the Ludlovian of the Welsh Borderland (Holland, Lawson, and Walmsley 1963), may have greater value in wider correlations, it is necessary that the faunas on which the work has largely been based, should be studied in detail and descriptions made available.

Very little work has been published on British Upper Silurian brachiopods since Davidson's Monograph of the last century. The writer had begun a study of Ludlovian enteletacean brachiopods based largely on his own collections from the Welsh Borderland when the opportunity to spend a year in the U.S.A. made possible the essential comparative studies.

Enteletacean brachiopods of the following genera occur in the Ludlovian rocks of the Welsh Borderland: *Isorthis*, *Salopina*, *Resserella* (= *Parmorthis*), *Dalejina* (= *Rhipidomelloides*), and *Dicoelosia*. The purpose of the present paper is to describe and figure the several species commonly determined as *Dalmanella orbicularis* (J. de C. Sowerby) and *D. lunata* (J. de C. Sowerby), important members of the successive faunal assemblages now recognized in the type Ludlovian (Holland, Lawson, and Walmsley 1959, Lawson 1960, Holland, Lawson, and Walmsley 1963).

Further papers are in preparation (jointly with Dr. A. J. Boucot and Dr. C. W. Harper) on the genera *Isorthis*, *Salopina*, *Resserella*, and *Fascicostella*, based on the study of Dr. Boucot's collection from the U.S.A., Canada, South America, Europe, and New Zealand. Examination of the enteletacean brachiopods in this collection, together with material kindly loaned by various museums and private individuals, has shown that, despite several references to the contrary, the species *I. orbicularis* and *S. lunata* have not yet been found outside the British area. In Britain, however, several isorthids, described here as new species and subspecies, have probably been confused as '*D. orbicularis*'. One of these new species (*I. clivosa*) has a wide distribution in Britain and occurs in North America (Maine and New Brunswick) and in South America (Venezuela).

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The species *Orthis lunata* and *O. orbicularis* were first described by J. de C. Sowerby in Murchison's *The Silurian System*, 1839, p. 611 and figured on pl. 5, figs. 15 and 16 respectively. Sowerby commented on the difficulty of distinguishing these species 'unless it [the specimen] be very perfect, or show the impressions upon the cast of the characteristic ridges in the interior'. It was presumably this difficulty which caused Davidson (1869, p. 215) to put *O. orbicularis* in synonomy with *O. lunata* and his figs. 1–5 on pl. XXVIII show both species under the latter name, an unfortunate error which misled several later authors. Elles and Slater (1906), however, in their account of the rocks of the Ludlow district, recognized and listed both species, as did subsequent authors in the Welsh Borderland. Several of these faunal lists, moreover, also recorded '*Dalmanella spp.*' from the Ludlovian—an indication that there were dalmanellid shells present, not easily assignable to either *D. lunata* or *D. orbicularis*.

The genus *Dalmanella* was erected by Hall and Clarke (1892) and the complex nomenclatorial history of this group has been recounted recently (Williams and Wright 1963, pp. 1–3). Since 1892, the species *O. lunata* and *O. orbicularis* have usually been assigned to *Dalmanella*, but in 1960 Boucot (*in* Boucot *et al.*, p. 3) erected the genus *Salopina* with *O. lunata* Sowerby as type species. Unfortunately the shell described and figured by him, in his pl. 1, figs. 6–12, is not *O. lunata* J. de C. Sowerby, but *S. submedia* (McLearn) from the Jones Creek Formation (? Wenlockian–Ludlovian in age) of New Brunswick, Canada. This species has now been redescribed in a joint paper on the 'Silurian Brachiopods and Gastropods of Southern New Brunswick' (Boucot, Johnson, Harper, and Walmsley—in press).

Kozlowski 1929, p. 75, erected *Isorthis* as a subgenus of *Dalmanella*, and described *I. szajnochai*, the type species, in considerable detail. Schuchert and Cooper 1932, pp. 149–50, redescribed *Isorthis* and raised it to generic rank. They assigned to it a number of American and European species but did not include *D. orbicularis*. Boucot (*in* Boucot *et al.*, 1960, p. 5 and pl. I, figs. 13–20, pl. II, figs. 1–7) described and figured a small silicified isorthid from the Sutherland River Formation (late Silurian–early Devonian age) of Devon Island, Canadian Arctic Archipelago, as *I. orbicularis* (Sowerby) and recorded it (p. 6) as the first known occurrence of this species from North America. I have been able to study this material in Dr. Boucot's collection and to determine that it is a new species quite distinct from *I. orbicularis* (J. de C. Sowerby), (Walmsley, Boucot, and Harper—in preparation).

In the present paper the genus *Salopina* is emended and *S. lunata* (J. de C. Sowerby) is described and figured. *O. orbicularis* J. de C. Sowerby is assigned to *Isorthis* emended, together with two new species and two new subspecies from the Welsh Borderland and a closely related species from Gotland—all of which are here described and figured.

MORPHOLOGICAL TERMINOLOGY

The terminology used by Schuchert and Cooper (1932) and defined in their glossary, pp. 6–11 and pl. A, is largely adopted. However, further explanation is needed of a few terms found necessary in the following systematic descriptions:

(*a*) *Fulcral plate*. This term was used by Schuchert and Cooper for a small concave plate connecting the brachiophore to the shell wall (see their pl. A, fig. 14), and considerable taxonomic importance was attached to the presence or absence of such a plate. It is

clear from their definition (p. 8, pl. A, fig. 14), that this name was applied to a plate which formed the floor of the socket and beneath which there was a small cavity. The antero-lateral edge of such a plate (being also the edge of the socket), shows itself in the usual figures of the interior of the brachial valve as a short line connecting the brachiophore and the hinge line. In such views it is usually impossible to determine whether a cavity exists beneath the socket floor. A very similar, if not identical, aspect is produced by an alternative structure which is commonly present in enteletacean shells. Here, the socket is a depression in the upper surface of a solid block or pad of calcite, but in this case, there is no cavity beneath the socket floor. The antero-lateral edge of such a structure resembles that of a true fulcral plate.

Since all morphologic stages can be seen between a true fulcral plate and a solid socket pad, it would appear that the leading edge of the socket may be formed either by forward extensions of the calcite forming the socket floor so as to overhang and eventually produce a lower cavity and a fulcral plate, or, possibly by resorption of the antero-lateral face of a solid socket pad which could produce a lower cavity and hence a fulcral plate. A third possibility exists. The socket pad condition may be a result of a true fulcral plate becoming submerged in adventitious calcite which has filled in the lower cavity.

It is not known which, if any, of these possible processes operated in the species here described, but from a purely descriptive point of view it is necessary to distinguish between the two common aspects. It is proposed therefore to restrict the use of the term fulcral plate to those situations where there is a lower cavity beneath the floor of the socket and to use the term socket pad where the floor of the socket is raised above the general surface of the valve but does not have a lower cavity beneath it.

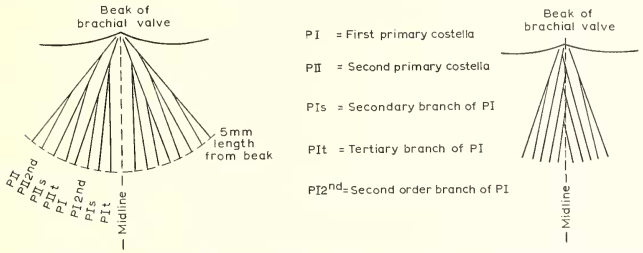
In their recent critical discussion of dalmanellid cardinalia, Williams and Wright (1963, pp. 4–11) also pointed out that transitional stages between fulcral plates and socket pads are to be expected. The useful term 'socket pad' is adopted from their paper.

(*b*) *Brachiophores.* This term is used to designate the plate-like structures which develop forward from the margins of the notothyrium, forming the inner (medial) margins of the sockets. No separate 'brachiophore processes' or 'brachiophore supports', terms used by Schuchert and Cooper, are distinguished.

(*c*) *Rib branching.* Although patterns of rib branching have been studied in the species here described, only minor differences occur and their taxonomic usefulness is outweighed by combinations of other morphological features. Nevertheless, the general pattern of branching in the medial region of the brachial valves of isorthids and salopinids has a character which immediately distinguishes these groups from *Resserella* [= *Parmorthis*], species of which have previously been confused with *I. orbicularis.* Davidson (1869, p. 218), for example, confused *O. orbicularis* (an isorthid) with *O. elegantula* (a resserellid) and found difficulty in convincing himself that *O. canaliculata* Lindstrom (again, an isorthid) was really different from *O. basalis* Dalman (a resserellid).

In *Isorthis* and *Salopina* the branching of the costellae in the medial area of the brachial valve is symmetrical about the shell's plane of symmetry. Secondary and sometimes tertiary branches of the medial primary pair, appear on the medial side. In *Resserella*, however, an unusual asymmetrical arrangement occurs in which the successive branches appear alternately to 'left' and 'right' of the preceding costella. This occurs in all known species of *Resserella* and is responsible for the unusual appearance of the ribbing in the

sulcus, to which several authors have referred—notably Schuchert and Cooper 1932, p. 129, in discussion of *Parmorthis*. Text-fig. 1 shows diagrammatically the typical arrangement of medial costellae on the brachial valve of isorthids and salopinids. The abbreviations used in the following systematic descriptions are explained in this diagram. The 5 mm. length stage is chosen as arbitrary, but convenient for this group of brachiopods. This figure also shows diagrammatically by contrast, the asymmetrical arrangement of the branching of medial costellae on the brachial valve of a resserellid shell. There are of course other generic distinctions, but the asymmetrical pattern of rib branching has not hitherto been recorded and is an easily observed external distinction.



TEXT-FIG. 1. Contrast in patterns of costellae bifurcation in *Isorthis* and *Salopina* (on left) and *Resserella* (on right), in the medial region of the brachial valve. Also, key to notation of costellae referred to in the text.

Number of ribs. The abundance, strength, and angularity of costellae as well as their branching patterns can be important distinguishing characters and various authors have attempted to record these features. However, since the number of costellae reaching the anterior margin in a branching system depends to a large extent on the stage of growth of the shell, figures given for the number of costellae, or even the number per mm., along the anterior margin are not meaningful unless the size of shell is also quoted. Rarely in description of enteletacean brachiopods have figures concerning the frequency of costellae been related to size. Where the frequency of costellae is referred to in the following descriptions it is taken as the average number per mm. at the 5 mm. length growth stage.

SYSTEMATIC DESCRIPTIONS

Superfamily ENTELETACEA Waagen 1884
[Nom. transl. Altskhova 1960 (*ex* Entelitinae Waagen 1884)]
Family SCHIZOPHORIIDAE Schuchert and LeVene, 1929
Subfamily SCHIZOPHORIINAE Schuchert and LeVene, 1929
Genus SALOPINA Boucot, 1960, emended

Type species. *Orthis lunata* J. de C. Sowerby *in* Murchison, 1839, p. 611, pl. 5, fig. 15.

Diagnosis. Relatively small schizophoriinids having a gently convex brachial valve, a more convex pedicle valve, hollow costellae, a poorly developed median ridge in the

pedicle valve and an adductor muscle field in which transverse ridges may be oblique and the margins meet the bases of the brachiophores in a sharp flexure.

Comparison. *Salopina* is distinguished from *Schizophoria* by having the pedicle valve always more convex than the brachial and by the absence of both a prominent median ridge in the pedicle valve and prominent antero-laterally directed transverse ridges in the adductor muscle field.

From *Isorthis*, *Salopina* is distinguished by its hollow costellae, and by the absence both of a distinct median ridge in the pedicle valve and of a strongly impressed adductor muscle field. The flexure by which the lateral margins of the adductor muscle field merge into the bases of the brachiophores in *Salopina* is distinct from the smooth continuity in the case of *Isorthis*.

The genus *Sphenophragmus* Imbrie 1959 also has hollow costellae and a general form very close to *Salopina* but is distinguished by its delicate cardinalia with a cardinal process raised on a notothyrial platform and the absence of a pronounced median ridge in the brachial valve. In the pedicle valve, the dental lamellae are not medially concave and there is no raised median area in the delthyrial cavity.

Description. Relatively small, subequally biconvex to almost plano-convex schizophoriinids with pedicle valve always having greater convexity. Brachial valve non-sulcate to gently sulcate. Outline variable from semicircular to subcircular or transversely elliptical. Hinge line straight, usually equal to about two-thirds of the greatest width, which is near mid-length. Lateral commissures straight to slightly flexed, anterior commissure crenulate and either rectimarginate or unisulcate. Pedicle valve interarea longer than interarea of brachial valve, usually gently curved, apsacline. Brachial valve interarea plane, anacline. Delthyrium and notothyrium open, latter usually partially filled by the myophore of the cardinal process. Pedicle valve beak usually distinct but not overhanging hinge line. Shell punctate, multicostellate with hollow costellae. Costellae increase by bifurcation and vary in degree of curvature as they radiate from the umbo. Costellae rounded to subangular. At 5 mm. length the number of costellae per mm. varies with species but is usually about three. The rate of appearance of secondary and tertiary branches varies with species.

Interior of pedicle valve. The muscle field is commonly weakly impressed, confined to the posterior half and the median third of the valve and in some species is even more restricted. No pronounced median ridge is present but there is a very faintly raised median area separating the elongate diductor tracks which are bounded laterally by low, forward extensions of the medially concave dental lamellae.

Teeth range in size with species and do not bear crural fossettes. Small lateral cavities external to the dental lamellae extend beneath the interarea. No pedicle callist present.

Interior of brachial valve. A commonly weakly impressed adductor muscle field, one-third or less the width of the valve, extends up to three-quarters of the valve length. A wide median ridge, at least a quarter as wide as the muscle field, separates the adductor impressions which are bounded laterally by not very pronounced, slightly raised margins sub-parallel to the median ridge. These margins become weaker as they curve to meet the median ridge in front of the muscle field. Posteriorly they are directed laterally to the brachiophores, but by a sharp flexure merge into the brachiophore bases (see Pl. 65, fig. 1). Faint transverse ridges directed normal to the median ridge or slightly antero-

laterally give a quadripartite aspect to the adductor field. The brachiophores vary in thickness and degree of divergence. Fulcral plates are present in most species, flooring triangular sockets beneath which are distinct, sometimes deep, lateral cavities.

The cardinal process has a short, thin shaft and a slightly bulbous simple non-lobed myophore bearing crenulations on its posterior face. Crenulations of the anterior margin of the shell are wide, low, flat or slightly rounded and bear a median groove. Interspaces are narrow and rounded. Crenulations commonly extend over one-fifth of the shell length.

Salopina lunata (J. de C. Sowerby)

Plate 64, figs. 15–27; Plate 65, figs. 1–12, 28, 29

1839 *Orthis lunata* J. de C. Sowerby *in* Murchison, p. 611, pl. 5, fig. 15 (non fig. 16) and pl. 3, fig. 12*d*.
1869 *Orthis lunata* Davidson, pp. 215–16, pl. 28, figs. 1, 2, 4 (non figs. 3, 3*a*), ? fig. 5.
non 1845 *Orthis lunata* Murchison, de Verneuil and Keyserling, Geol. de la Russie d'Europe, vol. 2, p. 189, pl. 13, figs. 6*a–d*.
non 1913 *Dalmanella lunata* Williams, *Proc. U.S. Nat. Mus.*, **45**, p. 337, pl. 3, figs. 1–5 and 8.
non 1922 *Orthis* (*Dalmanella*) *lunata* Barrois, Pruvost and Dubois, *Mém. Soc. géol. du Nord*, **6**, p. 77, pl. 11, figs. 4–12; p. 155, pl. 17, figs. 16–18.
non 1924 *Dalmanella lunata* McLearn, p. 55, pl. 4, figs. 5–6.
non 1960 *Salopina lunata* Boucot *et al.*, p. 3, pl. 1, figs. 6–12.

Diagnosis. Outline transversely elliptical to subquadrate, brachial valve sulcate with fine costellae which radiate with little curvature. Posterior costellae sub-parallel to hinge line in brachial valve. Brachiophores thin, long, pointed blades. Fulcral plates present.

Comparison. The New Brunswick shell figured by Boucot (1960, pl. 1, figs. 6–12) as *S. lunata* is now recognized as *S. submedia* (McLearn) which differs from *S. lunata* especially in the nature of the costellae. These are coarser and develop a distinct curvature which results in the most posterior costellae meeting the hinge line at a fairly high angle. *S. submedia*, which is redescribed in 'Brachiopods and Gastropods of Southern New Brunswick', Boucot, Johnson, Harper, and Walmsley (in press), also differs from *S. lunata* in its more circular outline and in the longer diductor impressions being bounded by less strongly curved dental lamellae.

Description. Unequally biconvex, pedicle valve having greater convexity and brachial valve sulcate. Outline transversely elliptical to subquadrate. Hinge line straight, equal to about three-fifths of greatest width which occurs slightly anterior to mid-length. Length equals about three-quarters of the width. Anterior commissure, crenulate and faintly unisulcate, lateral commissures straight.

Exterior of pedicle valve. Most convex in postero-median region, curvature decreasing toward lateral margins and slightly towards anterior margin. Outline subelliptical with anterior margin parallel to hinge line and lateral margins rounded, convex outwards. Cardinal angles obtuse and slightly less rounded than the antero-lateral margins. Beak projects one-tenth of the total length posterior to hinge line. Interarea triangular, with sharp lateral margins. Delthyrial margins subtending about 60°.

Exterior of brachial valve. The shallow sulcus extends from umbonal region to anterior margin where it equals about a quarter of greatest width. Anteriorly diverging margins of sulcus poorly defined. Valve outline subelliptical with anterior margin parallel to

hinge line, lateral margins rounded, convex outwards. Cardinal angles obtuse, less rounded than anterolateral margins. Interarea plane, anacline, about half as long as area in pedicle valve.

Rib branching pattern in median area shows P I (see text-fig. 1) quickly giving off secondary and second order branches towards midline. Secondaries give off tertiaries also medially, these being the most medial ribs on the valve. These do not arise together and points of branching can be one-fifth of the total length of valve apart. At 5 mm. length from the beak all these ribs have appeared, P II has also at this stage (5 mm.) produced secondary, tertiary and second order ribs so that increase in costellae is rapid.

Interior of pedicle valve. The muscle field is confined to the posterior one-third of the valve and is also one-third as wide as greatest width. A very faintly raised median region is flat and up to a quarter as wide as the muscle field. In some specimens it narrows towards the anterior. This may represent the adductor muscle track but no distinct scars are impressed. Diductor tracks on either side are elongate, semi-elliptical with anteriorly convex anterior margins slightly raised above the valve floor. Laterally the diductor impressions are bounded by the dental lamellae which diverge outwards before converging again as walls of the delthyrial cavity. The teeth are small, triangular in plan

EXPLANATION OF PLATE 61

Figs. 1–13. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, bank in field, 600 yards NW. of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825). 1–2, Internal mould of pedicle valve (×3), GSM 102206 and latex impression (×3). Note deep crural fossettes. 3–4, Internal mould of pedicle valve (×3), GSM 102207, Paratype and latex impression (×3). Note vascular trunks. 5, Internal mould of brachial valve (×3), GSM 102208. 6–7, Internal mould of brachial valve (×2), GSM 102209, and latex impression (×2). Note impressions of slightly crenulated sockets, thick brachiophores and their close proximity near the cardinal process. (See also figs. 20–21.) 8–9, Internal mould of brachial valve (×2), GSM 102210, and latex impression (×2). Note large brachiophores. 10–11, Internal mould of brachial valve (×2), GSM 102211, and latex impression (×2). 12–13, Internal mould of pedicle valve (×2), GSM 102212, and latex impression (×2).

Figs. 14–16. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, old quarry at Cwm, Usk inlier, Britain (Nat. Grid Ref. 33320160). 14, Internal mould of pedicle valve (×2), GSM 102213. 15, Latex impression of same specimen (×2). 16. Internal mould of brachial valve (×3), GSM 102214, Holotype.

Figs. 17–19. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, bank in field, 600 yards NW. of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825). 17, Internal mould of brachial valve (×2), GSM 102215. 18, Latex impression of same specimen (×2). 19, Oblique view of same latex impression showing divergence of brachiophores.

Figs. 20–30. *Isorthis amplificata* sp. nov., Wenlock Limestone old quarry on west side of Lincoln Hill, Iron Bridge, Britain (Nat. Grid Ref. 670038). 20–24, Anterior, posterior, side, internal and external views of brachial valve (×3), GSM 102216, Paratype. 25, Interior of pedicle valve (×2), GSM 102217. 26–30, Posterior, anterior, side, pedicle valve and brachial valve (×2), GSM 102218, Paratype.

Figs. 31–38. *Isorthis clivosa* sp. nov., 31–32, Mid Eltonian siltstone, trackside 300 yards south of Hafod-fawr, Llandovery area, Britain (Nat. Grid Ref. 81443096), internal mould of pedicle valve (×2), GSM 102219, and latex impression (×2). 33–34, Mid-late Eltonian, 6 yards upstream of mountain fence along Nant Cwm Clyd, 1,000 yards SE. of Cwm Clŷd Farm, Llandovery area, Britain (Nat. Grid. Ref. 80152980), internal mould of brachial valve (×2), GSM 102220, and latex impression (×2). 35–38, Mid Eltonian, 50 yards up R. Gwydderig from Bont Wen, on road A. 40. 35–36, External mould of pedicle valve (×2), GSM 102221, and latex impression (×2). 37–38, External mould of brachial valve (×2), GSM 102222, and latex impression (×2).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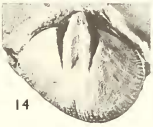
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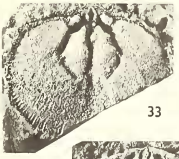
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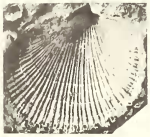
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and section and project normal to the hinge line. External to the teeth are lateral cavities roofed over by the interarea and bounded by the external face of the tooth and the floor of the valve. In large specimens these cavities may be obscured.

Interior of brachial valve. The adductor muscle field extends about four-sevenths of the distance to the anterior margin and is slightly less than one-third as wide as the greatest shell width. A rounded, median ridge (about two-fifths width of muscle field) extends from the anterior margin of the muscle field posteriorly becoming somewhat carinate as it passes between the brachiophores. Flanking the median ridge are adductor impressions, narrower than the median ridge and bounded by very faintly raised margins which are sub-parallel to the median ridge, but slightly concave towards it. Posteriorly these margins, which are directed externally to the brachiophore bases, curve sharply medially and merge with the bases of the brachiophores. Anteriorly the margins fade towards the end of the median ridge. Anterior adductor impressions are smaller than the posterior pair and when slightly more impressed are clearly separated by faint transverse ridges. In many specimens the impressions are faint, the outer margins incomplete and the appearance is of divergent margins extending from immediately outside the brachiophores, fading about mid-length where the median ridge also may fade.

The brachiophores are very long, thin, erect, pointed blades directed normal to the hinge line or only slightly divergent from each other. Their distal extremities are separated by a distance equal to one-fifth of greatest shell width. Their anterior edges are normal to the commissural plane. Proximally they are connected by short curved fulcral plates to the posterior edge of the valve floor along the hinge line. The fulcral plates floor very small sockets and roof over a much larger lateral cavity.

The cardinal process consists of a thin blade-like shaft which arises from the crest of the posterior carinate portion of the median ridge between the brachiophores and terminates in a very slightly bulbous, non-lobed myophore.

Anterior crenulations on the valve margin have a low rectangular cross-section and bear fine grooves along the mid-line of their internal faces. Interspaces are rounded. This type of anterior crenulation is very similar to that described as diagnostic of *Rhipidomelloides*.

Type specimens. This species was erected and first described by J. de C. Sowerby in Murchison's *Silurian System*, p. 611, and illustrated in pl. 3, fig. 12*d* and pl. 5, fig. 15.

Boucot (1960, p. 3) designated as 'holotype', 'The specimen figured by Salter (op. cit.)', referring to pl. 5, fig. 15.

The figure was by J. de C. Sowerby, not Salter, and comprised not one but three specimens, an internal impression of a pedicle valve, an internal impression of a brachial valve and an external impression of a pedicle valve. None of the originals of these figures has been definitely identified but they may be related to GSM 51555 in the Geological Survey Museum, London. Specimen No. GSM 51555 is from the Geological Society Collection—Murchison Collection, Oaker Quarry (near Beecher) and the old label states 'Pl. 5, fig. 15'. The impressions are all slightly distorted. Similar distortion is to be seen in specimens from Oaker Quarry (Nat. Grid reference 377816) about 5 miles east of Clun, but not in material from the Ludlow district or the inliers of Woolhope, May Hill, or Usk. Dr. Stubblefield (in correspondence) considers that this specimen is remotely eligible as the original of pl. 5, fig. 15, and is quite probably one of several syntypes. In order to clarify the situation, I designate the ringed specimen on GSM 51555 (an internal impression of a brachial valve) as lectotype and figure it Plate 65, fig. 28. It is arguable whether a specimen which is not certainly the original should be designated lectotype. However, the Geological Society Collection has been very carefully examined by the Geological Survey and it seems certain that no more likely specimen exists. To designate GSM 51555 as a neotype would hardly assign to this specimen its due significance.

Distribution. S. lunata ranges in the Ludlovian of Britain from the Lower Leintwardinian to the highest Whitcliffian where it is most abundant. In the inliers of Usk, May Hill, and Woolhope it has been recorded as present but very rare in the basal part of the Downtonian—immediately above the Ludlow Bone Bed. It should be noted that the original of Sowerby's pl. 3, fig. 12*d*, also of *S. lunata*, cannot be traced, but the tablet bearing specimens figured as 12*a*, *b*, *c*, *e*, and *g* is marked: 'Devonian (Tilestones) Horeb Chapel, R. I. Murchison, F.G.S.'.

In the Lower Leintwardinian, it is present at May Hill and Ludlow, rare at Usk and fairly common at Woolhope. In the Upper Leintwardinian it is fairly common at May Hill, Usk, Ludlow, and Builth, and common at Woolhope. In the Lower Whitcliffian, it is rare in the Leintwardine area, fairly common at Woolhope, Ludlow and Builth, and common at Usk and May Hill. In the Upper Whitcliffian, it is common at Usk, May Hill, Woolhope, Ludlow, the Leintwardine area, Builth, Knighton, and Kerry. It appears, therefore, to have migrated from the south-eastern part of the shelf area north-westwards to the basin area during the later part of Ludlovian time. (See also Holland and Lawson, 1963, p. 287.)

Records of *S. lunata* from localities outside Britain have been checked and cannot be authenticated. Its sudden appearance in Britain in early Leintwardinian times raises the question of its ancestry. In the Hemse Group of Gotland (early Ludlovian age, probably mid Eltonian based on associated *Pristiograptus nilssoni* and *Lobograptus scanicus*), is a shell which is considered to be conspecific with *D. conservatrix* McLearn. The latter is a salopinid and is redescribed in 'Salopinid Brachiopods of the Silurian and Lower Devonian' (Walmsley, Boucot, and Harper, in preparation). *S. conservatrix* is known from the Ross Brook Formation (late Llandovery age) of Nova Scotia. *S. conservatrix* seems to be the most likely ancestor of *S. lunata*.

A species of *Salopina* from the Stonehouse Formation (Gedinnian age) of Arisaig, Nova Scotia, (Walmsley, Boucot and Harper, in preparation) is very close to *S.* [*Dalmanella*] *missendenensis* (Straw), from the Little Missenden Bore (1913) material. Unfortunately, there is too little bore material available to establish specific identity. The age of the bore material was recorded, Straw and Woodward 1933, p. 139, as 'either late Downtonian or post-Downtonian'. It seems likely that both the Stonehouse and Little Missenden forms were derived from *S. lunata*.

Subfamily ISORTHINAE Schuchert and Cooper, 1931
Genus ISORTHIS Kozlowski, 1929, emended

Type species. I. szajnochai Kozlowski, 1929.

Diagnosis. Planoconvex to equally biconvex isorthinids lacking hollow costellae, having a well-developed median ridge separating elongate diductor tracks in the pedicle valve, and a well-impressed adductor muscle field in which the transverse ridges are normal to the median ridge in the brachial valve. Cardinal process commonly simple, non-lobed especially in Silurian species, bilobed in some Devonian species. Brachiophores erect or postero-laterally inclined, never convergent on to the median ridge.

Comparison. Isorthis is distinguished from *Schizophoria* by having the greater convexity always in the pedicle valve and by having transverse ridges in the adductor muscle field aligned normal to the median ridge whereas in *Schizophoria* they are oblique, directed antero-laterally from the median ridge and the brachial valve has the greater convexity. Schuchert and Cooper (1932, p. 149) suggested that *Isorthis* was probably derived from an early Silurian *Schizophoria*. No true *Schizophoria* is known, however, from the Silurian and it appears more likely that *Schizophoria* in the Devonian was in fact derived from *Isorthis*.

Salopina is distinguished from *Isorthis* by having hollow costellae (see Boucot *et al.* 1960, pl. 1, fig. 12) and by the distinctive flexure where the margins of the adductor muscle field meet the bases of the brachiophores (see Pl. 65, fig. 1 and contrast with Pl. 63, figs. 10 and 14). The median ridge in the pedicle valve is also less pronounced.

The distinction between *Isorthis* and both *Dalmanella* and *Onniella* as emended by Williams and Wright (1963, pp. 27, 28) lies mainly in the shorter more cordate pedicle muscle field of the latter genera and in the case of *Dalmanella* the convergence of the brachiophore bases on to the median ridge.

Levenea is distinguished from *Isorthis* by its pentagonal delthyrial cavity and muscle field in the pedicle valve.

Description. Biconvex, varying from almost planoconvex to subequally biconvex. Pedicle valve always having greater convexity. Brachial valve non-sulcate to sharply sulcate. Outline variable, sub-circular, transversely elliptical or shield shaped. Hinge line straight, usually between half and three-quarters as long as greatest shell width, which is near mid-length. Lateral commissures straight, anterior commissure recti-marginate and crenulate or unisulcate and crenulate. Pedicle valve interarea usually twice as long as brachial valve interarea, gently incurved, apsacline. Delthyrium triangular, open. Brachial valve interarea plane, anacline to orthocline. Notothyrium triangular, open, partially filled by cardinal process. Pedicle valve beak distinct but not overhanging hinge line, brachial valve beak slight. Shell multicostellate, costellae increasing by bifurcation. Pattern of bifurcation in medial region of brachial valve characterized by median pair of primary costellae branching medially very early. In some species these secondary costellae again branch medially to produce tertiary costellae. A second order of branching from the median primary may arise. The second pair of primary costellae produce secondaries and both primary and secondary costellae may again divide producing tertiaries and second order branches. At 5 mm. length the presence of tertiary and second order branching varies with species. All this branching is symmetrical as in *Salopina*, but quite different from the pattern developed in *Resserella*. The costellae are rounded, evenly spaced with rounded interspaces (striae). At 5 mm. length the number of costellae per mm. varies between three and five and is most commonly four.

Interior of pedicle valve. The delthyrial cavity is usually fairly deep, but may have a delthyrial platform on which the median ridge and diductor tracks are raised above the general floor of the valve. In some species the anterior edge of the platform makes a steep descent. Dental lamellae vary in thickness and in their inclination relative to the plane of symmetry of the shell. A pedicle callist is present in some species. Teeth, triangular in plan and cross-section project normal to the hinge line, sometimes curving slightly posteriorly. Crural fossettes are usually present and vary in depth and position on the medial surface of the tooth. A median ridge extends from the delthyrial cavity, not reaching beyond the diductor impressions. The ridge varies in length, height, and width and may be parallel sided, narrow anteriorly, or widen anteriorly. In some species subelliptical adductor impressions occupy the posterior end of the ridge. In others no distinct adductor impressions are visible but faint striations along the median ridge may represent an adductor track. Diductor tracks, separated by the median ridge, may be slightly or deeply impressed, narrow, elongate, sub-parallel or divergent anteriorly, rarely extending beyond mid-length. The diductor impressions have a smooth, non-flabellate outline and do not enclose the adductor impressions anteriorly.

Pallial marking rarely visible. In some species vascular trunks extend forward from the anterior limit of the diductor tracks, diverging in line with these tracks, towards the anterior margin.

Crenulations of the anterior shell margin usually low and rounded but variable.

Interior of brachial valve. The sub-circular to elongately elliptical adductor muscle field occupies the median third of the valve, usually extending slightly anterior to mid-length. A median ridge is always present varying from one-eighth to one-quarter as wide as the muscle field, usually constant in width, rarely tapering anteriorly. The degree of impression of the muscle scars varies, resulting in some species in a distinct transverse 'step' or ridge normal to the median ridge, separating the anterior and posterior pairs of impressions and giving a clearly quadripartite appearance, with the anterior pair either equal to or larger than the posterior pair. In other species there is no sign of such transverse marking. The muscle field is bounded by a raised margin of variable outline which anteriorly converges and fades towards the median ridge and posteriorly merges smoothly with the bases of the brachiophores.

The brachiophores vary in angle of divergence, thickness, and length. In most species they are thin, flaring plates. Fulcral plates connect the lateral face of the brachiophore to the posterior margin of the valve and floor the dental sockets which vary in size. In some shells, socket pads are present instead of fulcral plates. The cardinal process

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EXPLANATION OF PLATE 62

Figs. 1–22. *Isorthis clivosa* sp. nov. 1–4, Mid Eltonian siltstone, trackside 300 yards SE. of Hafod-fawr, Llandovery area, Britain (Nat. Grid Ref. 81443096). 1–2, Internal mould of brachial valve (×2), GSM 102223, and latex impression (×2). 3–4, Internal mould of pedicle valve (×2), GSM 102224, and latex impression (×2). 5–6, Early Leintwardinian, roadside quarry, 1,080 yards ENE. of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 49107399), internal mould of pedicle valve (×2), GSM 102225, and latex impression (×2). 7–8, Early Bringewoodian, roadside on A. 40, 190 yards WNW. of Ynys-y-Bont, Llandovery area, Britain (Nat. Grid Ref. 83723225), internal mould of pedicle valve (×2), GSM 102226, and latex impression (×2). Note vascular trunks. 9–10, Early Bringewoodian, roadside, 1,000 yards east of Sluvad Farm, Usk inlier, Britain (Nat. Grid Ref. 32509920), internal mould of pedicle valve (×3), GSM 102227, and latex impression (×3). Note crural fossettes, thick dental lamellae, and wide median ridge. 11–12, Mid Eltonian, trackside, 300 yards south of Hafod-fawr, Llandovery area, Britain (Nat. Grid Ref. 81443096), internal mould, of brachial valve (×2), GSM 102228, Paratype. Note pear-shaped outline of adductor muscle field, and latex impression (×2). 13–14, Early Bringewoodian, roadside on A. 40, 190 yards WNW. of Ynys-y-Bont, Llandovery area, Britain (Nat. Grid. Ref. 83723225), internal mould of pedicle valve (×2), GSM 102229, Paratype, and latex impression (×2). Note abrupt end of median ridge. 15–18, Mid Eltonian, stream bank 600 yards SE. of Esgair llaethdu, Llandovery area, Britain (Nat. Grid Ref. 79022926). 15–16, Internal mould of pedicle valve (×2), GSM 102230, Paratype, and latex impression (×2). 17–18, Internal mould of pedicle valve (×3), GSM 102231, and latex impression (×3). 19–20, Late Leintwardinian, roadside, 1,230 yards ENE. of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 49227407), internal mould of pedicle valve (×3), GSM 102232, Holotype, and latex impression (×3). Note flat median ridge with abrupt anterior end and also the anterior crenulations. 21–22, Mid Eltonian, trackside 300 yards south of Hafod-fawr, Llandovery area, Britain (Nat. Grid Ref. 81443096), external mould of pedicle valve (×2), GSM 102233, and latex impression (×2).

Figs. 23–35. *Isorthis slitensis* sp. nov. 23–27, Slite Marl (Wenlockian), Cement plant quarry at Slite, Island of Gotland (Baltic), pedicle valve, side, brachial valve, anterior and posterior views (×2), GSM 102234, Paratype. 28–32, Slite Marl, canal ditch 800 m. SW. of Alby (north of Lergravsviken), Parish of Rute, Gotland, exterior, interior, anterior, posterior, and side views of brachial valve (×2), GSM 102235, Holotype. Note relatively long adductor muscle field and vascular marks. 33–35, Slite Marl, Cement plant quarry at Slite, Gotland. 33, Interior of pedicle valve (×2), GSM 102236, Paratype. 34, Interior of pedicle valve ×(3), GSM 102237. Note relatively long diductor tracks and median ridge. 35, Interior of pedicle valve (×3), GSM 102238. Note anterior crenulations.


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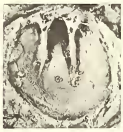
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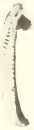
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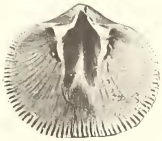
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arises as a thin laterally compressed or semi-cylindrical shaft from the median ridge between the brachiophores and expands slightly into a myophore which may be simple, non-lobed, and slightly bulbous, occupying the apical portion of the notothyrium, or may be distinctly bilobed as in several Devonian species. In well-preserved specimens the posterior face of the myophore often shows a series of chevron-shaped crenulations arranged with their apices pointing anteriorly.

Geological Range. Silurian (Lower Llandoverian) to Devonian (Eifelian, ? Lower Givetian).

Remarks. Kozlowski (1929, pp. 29 and 75) regarded the near equality of the convexity of the two valves and the simple cardinal process as being amongst the distinguishing characteristics of *Isorthis*. Schuchert and Cooper (1932, p. 149) described the lateral profile as 'unequally to sub-equally biconvex' and stated that the cardinal process was 'small, bilobed, trilobed or multilobed'.

In the twenty species of *Isorthis* which have been studied, the biconvexity varies from almost plano-convex to sub-equally convex. Silurian species generally have a simple cardinal process. Some Devonian species have a bilobed process.

Isorthis orbicularis (J. de C. Sowerby)

Plate 63, figs 1–15; Plate 64, figs. 1–14; Plate 65, figs. 30–31

1839 *Orthis orbicularis* J. de C. Sowerby *in* Murchison, p. 611, pl. 5, fig. 16 (non fig. 15).
non 1924 *Dalmanella orbicularis* McLearn, p. 56, pl. 4, fig. 7.
non 1942 *Dalmanella orbicularis* Dahmer, *Senckenbergiana*, **25**, p. 116, figs. 14–16.
non 1951 *Dalmanella orbicularis* Dahmer, pp. 91–94, pl. 7, fig. 1; pl. 9, figs. 20–21; pl. 10, fig. 6; pl. 11, fig. 22; pl. 12, fig. 10.
non 1960 *Isorthis orbicularis* Boucot *et al.*, p. 5, p. 1, figs. 13–20; pl. 2, figs. 1–7.

Diagnosis. Unequally biconvex, sulcate, with circular to transversely elliptical outline. Median ridge of pedicle valve narrow, rounded, extending to centre of valve and separating sub-parallel diductor tracks which do not extend into anterior half of valve. Posteriorly, the median ridge separates a pair of short semi-elliptical adductor impressions.

Brachial valve adductor muscle field well impressed, bounded by sub-circular raised margin, confined to posterior half of valve and distinctly quadripartite. Median ridge relatively wide and constant in width, posteriorly thickened between brachiophores. Muscle impressions sub-equal. Brachiophores short, divergent, and slightly flaring blades. Cardinal process non-lobed.

Comparison. The distinctions between *I. orbicularis* and the other isorthids described in this paper are given under the respective species. *I. orbicularis* has been confused with *Salopina lunata* but these are now seen to represent different genera. *I. orbicularis* has also been confused with *I. fornicatumcurvata* Fuchs. The more elongate and less distinctly, less constantly quadripartite adductor muscle field of the later species, however, together with greater convexity of the brachial valve, clearly distinguish it.

Description. Unequally biconvex to almost plano-convex, with pedicle valve at least twice as deep as brachial valve. Circular to transversely elliptical outline with well-

rounded cardinal angles. Anterior commissure crenulate and slightly sulcate, lateral commissure straight. Hinge line equal to two-thirds of greatest width, which is at mid-length. Width slightly greater than length, thickness almost half length.

Exterior of pedicle valve. Evenly convex with distinct beak projecting one-sixth total length posterior to hinge line. Delthryium margins subtending about 60°. Lateral margins of the interarea smoothly rounded.

Exterior of brachial valve. Slightly convex with shallow median sulcus widening from umbo to anterior margin where it equals about one-third of shell width. Lateral margins of sulcus not sharply defined. Outline, sub-circular to transversely elliptical with antero-lateral margins rather more rounded than postero-lateral margins. Interarea anacline. Notothyrium enclosing about 60°.

The pattern of rib branching in the median area of the brachial valve consists of a median pair of P I, with P Is, P It and P I 2nd, and P II with P IIs. At 5 mm. length all these except sometimes P It, have appeared (see text-fig. 1).

Interior of pedicle valve. A low, rounded, narrow median ridge extends from the delthyrial cavity to almost mid-length where it fades gradually. In the posterior part of the delthyrial cavity this ridge separates short subelliptical adductor scars, often well impressed. Anterior to the adductor impressions the sub-parallel diductor tracks are separated by the median ridge and end with rounded margins at mid-length. Laterally the diductor tracks are bounded by straight sub-parallel or slightly convergent ridges which extend forward from the dental lamellae, decreasing in height to mid-length.

The teeth, which bear crural fossettes on their medial surfaces, are supported by dental lamellae which diverge slightly ventro-laterally before converging towards the floor of the delthyrial cavity. A small pedicle callist is present.

Interior of brachial valve. The well-impressed adductor muscle field is confined to the posterior half of the valve, and is bounded by a circular to slightly elongate raised margin, which merges posteriorly with the bases of the brachiophores and anteriorly fades as it curves towards the median ridge. A less well-developed pair of ridges runs antero-laterally from the junction of the anterior and posterior pairs of adductors. Four adductor impressions of sub-equal size are separated by a broad, low, rounded median ridge which is about one-quarter to one-third as wide as the muscle field and by narrower transverse ridges which are either parallel to the hinge line or directed slightly postero-laterally. This arrangement of ridges separating the muscle impressions gives a distinctive 'cross' pattern. Short, stubby, plate-like brachiophores flare antero-laterally. Antero-laterally directed sockets are supported by fulcral plates or, often in larger specimens, by socket pads.

The cardinal process has a cylindrical shaft and a conical non-lobed myophore.

Anterior crenulations are low, rounded without median grooves and are evenly spaced. Pallial marks are rarely seen but a pair of trunks running anteriorly from the adductor impressions divide before reaching the anterior margin. From the same origin a second pair run lateral to them.

Variation in muscle field. Most variation occurs in the brachial muscle field where the highly symmetrical cross pattern may be extended to an elongate, roughly elliptical outline with irregularly raised margins and transverse ridges which are obscure or faint, depending upon the degree of impression of the muscle scars. The pedicle valve shows some slight variation in the ridges bounding the diductor tracks. These ridges may be

straight and almost parallel, straight but slightly convergent anteriorly, or slightly curved (convex outwards).

Type specimens. This species was first described by J. de C. Sowerby (*in* Murchison, *Silurian System*, p. 611). It was figured pl. 5, fig. 16 which is a multiple figure. The figured specimens are in the collection of the Geological Survey and Museum of Great Britain and are believed to be related to fig. 16 as follows:

Geol. Soc. Colln. No. 6647 is taken to be the original of pl. 5, fig. 16, top left. Geol. Soc. Colln. No. 6648 is thought to be the original of fig. 16, bottom left, top right, and bottom right, but GSM 33239 may also have been used in drawing fig. 16, bottom right.

Geol. Soc. Colln. No. 6647 is a poorly preserved internal mould of a pedicle valve. Geol. Soc. Colln. No. 6648 is a complete shell and GSM 33239 is a poorly preserved exterior of a brachial valve.

In his brief description of *O. orbicularis*, J. de C. Sowerby (*Silurian System*, p. 611) mentions many localities in the Welsh Borderlands, but does not state the horizon or localities from which his specimens figured in pl. 5, fig. 16 were obtained.

Davidson (1869, pp. 215 and 218) included this species in *O. lunata*. McLearn (1924, p. 56) records *D. orbicularis* (J. de C. Sowerby) as occurring rarely in boulders in Stonehouse field at Arisaig, Nova Scotia—'probably from zone D of the Stonehouse Formation'. From his illustration pl. 4, fig. 7, it is not possible to say whether this is *I. orbicularis* but examination of a large collection of material from the Stonehouse Formation has failed to reveal a single specimen of *I. orbicularis*. *I.* cf. *fornicatumcurvata* Fuchs, however, not referred to by McLearn is fairly abundant—and it seems likely that this record of *I. orbicularis* from Arisaig is mistaken.

Dahmer (1951, p. 91) stated that the type was the specimen figured in *Silurian System*, pl. 5, fig. 16, but quoted two specimen numbers, 6647 and 6648, and referred to 'the figured ventral valve'. No. 6647 is a pedicle valve but 6648 is a complete shell. His selection of a type is thus not clear and in order to clarify the situation, Geol. Soc. Colln. No. 6647 is here selected as the lectotype. Geol. Soc. Colln. No. 6648 and GSM 33239 are figured syntypes. Specimens numbers 6647 and 6648 are refigured, pl. 65, figs. 30 and 31. It should be noted, however, that the species from the Ebbe Sattel of Germany described and figured by Dahmer as *D. orbicularis* is a different species, *I. fornicatumcurvata* (Fuchs). Despite the fact that Dahmer put this latter species in synonomy with *I. orbicularis*, the two species are quite distinct, as detailed under Comparison, above p. 465.

Boucot, *et al.* (1960, p. 5, pl. 1, figs. 13–20 and pl. 2, figs. 1–7) described a species from the Sutherland River Formation of Devon Island (Canadian Arctic Archipelago), as *I. orbicularis* and recorded the occurrence as the first known from North America. Examination of these silicified shells has revealed, however, that they differ in a number of important characteristics from *I. orbicularis*. In particular, the absence of a sulcus; the lack of transverse ridges and the faintness of the median ridge in the brachial muscle field, which is thus not distinctly quadripartite and is only weakly impressed; the relatively shorter hinge line and the narrow double median ridge in the pedicle valve (see Boucot, pl. 2, fig. 3).

Distribution. I. orbicularis is a common shell in the shelly facies of the Ludlovian of the Welsh Borderland. It ranges from the base of the Ludlovian (lowest Eltonian) to the lower part of the Whitcliffian but is most abundant in the lower Leintwardinian. In the basin facies of the Ludlovian in Central Wales, it has been recorded as common in the 'lower siltstone group' (see Lawson, 1960, p. 121), and rare or absent above the zone of *Monograptus leintwardinensis*.

It has been recorded from several places outside Britain but examination of Boucot's collections from Gotland, Germany, Podolia, New Brunswick, Nova Scotia, Quebec and Maine reveals that the isorthids in these areas are different species from *I. orbicularis*, several of them being new species which are being described in a separate paper. So far, no specimens of *I. orbicularis* (J. de C. Sowerby) have been seen by the author from localities outside the Welsh Borderland.

Isorthis slitensis sp. nov.

Plate 62, figs. 23–35.

Diagnosis. Unequally biconvex, faintly sulcate, sub-circular outline with only slightly rounded cardinal angles. Median ridge of pedicle valve narrow, carinate to rounded,

extending into anterior half of valve and separating wide parallel diductor tracks. Brachial valve adductor muscle field moderately well impressed, bounded by circular raised margin, extending into anterior half of valve, distinctly quadripartite, muscle impressions of equal size. Median ridge of constant width, thickened posteriorly between brachiophores. Brachiophores moderately thick, straight, divergent blades.

Comparison. This species is very close to *I. orbicularis*, but is distinguished by having the following: (i) less circular outline with less rounded cardinal angles, (ii) sulcus less defined, (iii) the valves of almost equal length, (iv) both pedicle and brachial valve muscle fields relatively longer, extending into the anterior half of the shell.

Description. Unequally biconvex to almost plano-convex with pedicle valve at least twice as deep as the brachial valve. Circular to sub-quadrate outline with cardinal angles only slightly rounded and antero-lateral margins well rounded. Anterior commissure crenulate, slightly sulcate, lateral commissures straight. Hinge line equal to two-thirds of greatest width which is at mid-length. Width slightly greater than length, thickness slightly more than half of the length.

Exterior of pedicle valve. Evenly convex with distinct beak which barely projects posterior to the brachial valve. Lateral margins of the interarea smoothly rounded. Margins of delthyrium enclosing 60°.

Exterior of brachial valve. Slightly convex with faint median sulcus widening anteriorly. Outline somewhat shield-shaped with cardinal angles only slightly rounded. Interarea anacline. Notothyrium enclosing about 70°, partially filled by the cardinal process which protrudes slightly. The branching of the costellae in the median area of the brachial valve results in P I and P II having P Is and P IIs at 5 mm. length. Tertiary and second order branches appear only at or after this stage.

Interior of pedicle valve. A median ridge, carinate in small forms, becoming rounded in larger shells, extends from the delthyrial cavity to about mid-length of the valve where it ends in a gradual slope. In one large shell the median ridge bears a very faint median groove on its posterior two-thirds. No separate adductor impressions are seen. Parallel diductor tracks which extend beyond the anterior end of the median ridge and are separated by it, terminate imperceptibly just anterior to mid-length. Laterally the diductor tracks are defined by low ridges extending forward from the bases of the dental

EXPLANATION OF PLATE 63

Figs. 1–15. *Isorthis orbicularis* (J. de C. Sowerby). 1–4, Early Leintwardinian, south end of old quarry, behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 1, Internal mould of pedicle valve (×3), GSM 102239. Note impressions of adductor and diductor muscles. 2, Latex impression (×3) of same specimen. Note diductor tracks confined to posterior half of valve. 3, Enlarged view (×5) showing adductor and diductor impressions and subparallel dental lamellae. 4, Side view of specimen in fig. 1, showing absence of delthyrial platform. 5–8, Early Bringewoodian, roadside quarry at Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 35209780), posterior view (×3), internal mould of pedicle valve (×2), GSM 102240, latex impression (×2) and enlarged (×5). Note adductor scars in relation to the narrow median ridge. 9–15, Early Leintwardinian, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 9–10, Internal mould of brachial valve (×2), GSM 102241, and latex impression (×2). 11–12, External mould of brachial valve (×2), GSM 102242, and latex impression (×2). 13–15, Internal mould of brachial valve (×2), GSM 102243, latex impression (×2) and enlarged view of mould (×5). Note adductor muscle field confined to posterior half of valve and also vascular trunks.


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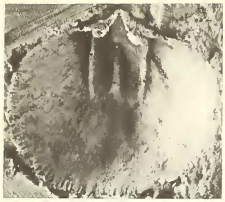
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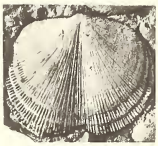
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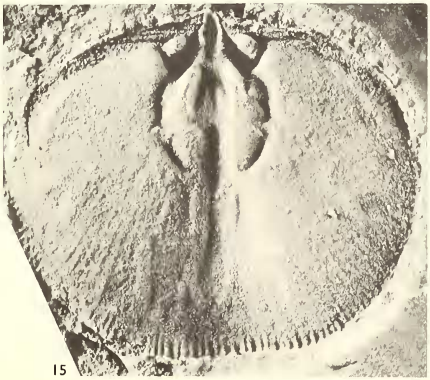
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lamellae. The ridges terminate opposite the anterior end of the median ridge. The teeth are strong, have a rounded lateral profile, and deeply incised crural fossettes on the anterior edges of their medial faces. Dental lamellae diverge slightly outwards before converging slightly towards the floor of the delthyrial cavity. A small pedicle callist is present.

Interior of brachial valve. Well-impressed adductor muscle scars form a distinct quadripartite pattern surrounded by a circular to slightly elongate raised margin, the lateral portions of which fuse with the brachiophore bases. Anteriorly the raised margin decreases as it curves in towards the median ridge. The median ridge, which is broad and low, equals about one-quarter of the width of the muscle field. Transverse ridges caused by the deeper impressions of the anterior pair of muscle scars are parallel to the hinge line. The muscle scars are of equal size.

The brachiophores diverge from the inner margins of the notothyrium, with a slight flare, at about 74° from each other. They are fairly thick stubby plates with a carinate posterior edge and bluntly rounded extremities. The postero-lateral faces of the brachiophores merge into fulcral plates which floor the sockets or into socket pads. The triangular sockets widen antero-laterally and are slightly roofed over at the posterior end by the interarea. The cardinal process, which arises from a posterior thickened and raised portion of the median ridge (notothyrial platform), has a short, thick cylindrical shaft and a conical myophore which largely fills the notothyrium from which it protrudes slightly. This projecting posterior portion of the myophore bears five or six fine crenulations arranged in a chevron pattern with apices directed anteriorly. Along the anterior margin of the valve, the crenulations are low and rounded with narrower interspaces.

Holotype. GSM 102235, brachial valve (figured Pl. 62, figs. 28–32). Slite Marl (Wenlockian). Canal ditch 800 m. south-west of Alby (north of Lergravsviken), parish of Rute, Gotland.

Paratypes. GSM 102234, whole shell (figured Pl. 62, figs. 23–27); GSM 102236, pedicle valve (figured Pl. 62, fig. 33); GSM 102237, pedicle valve (figured Pl. 62, fig. 34); and GSM 102238, pedicle valve (figured Pl. 62, fig. 35). Slite Marl (Wenlockian). Cement plant Quarry at Slite, Gotland.

Distribution. This species has only been seen in material collected by Boucot from the Slite Marl of Gotland. Additional material was kindly provided by Dr. Hede from the same beds but from a different locality. It is not present in collections available from other horizons in Gotland, nor is it present in collections from other areas. The age of the Slite Marl is given (Regnell and Hede, 1960, p. 49) as Wenlockian. According to Boucot (verbal communication) it is probably—but not certainly—Upper Wenlockian. The close similarity between *I. slitensis* of Wenlockian age and *I. orbicularis* of Ludlovian age suggests that the latter may have been derived from the former. It is also the reason for including a Gotland shell in this paper as comparisons are thereby made easier.

Isorthis amplificata sp. nov

Plate 61, figs. 1–30

1869 *Orthis crassa* Lindstrom; Davidson, p. 213, pl. 27, figs. 18 and 19*a* (non fig. 17).

Diagnosis. Unequally biconvex, faintly sulcate with circular to transversely elliptical outline Median ridge of pedicle valve low, flat, moderately wide for about one-third of the valve length then tapering gently; separating diductor tracks which do not reach mid-length.

Brachial valve adductor muscle field well impressed, bounded by circular raised margin extending well into anterior half of valve; distinctly quadripartite. Median ridge

narrows between larger anterior pair of impressions, and posteriorly thickens between the brachiophores. Brachiophores distinctive, very thick, straight, erect, only slightly divergent; their posterior edges separated only by the width of the cardinal process. Sockets large and deep; teeth massive.

Comparison. This species is fairly close to *I. orbicularis* but is distinguished by the following:

(i) Unusually thick non-flaring brachiophores which almost meet at their bases and which have a posterior edge aligned normal to the commissure plane, whereas in *I. orbicularis* the posterior edge is only slightly oblique to this plane and the brachiophores are thinner and flare outwards as they diverge.

(ii) More massive teeth with deeper crural fossettes and larger sockets.

(iii) The wider median ridge and absence of distinct adductor scars in the pedicle valve.

(iv) Pear-shaped outline of the muscle field in the brachial valve.

There is an amplification, especially of teeth and brachiophores, to which the name refers.

Description. Unequally biconvex, with pedicle valve twice as deep as brachial valve. Outline sub-circular to transversely elliptical with rounded cardinal angles. Anterior commissure crenulate and gently sulcate, lateral commissure straight. Hinge line slightly greater than half the greatest width which is slightly posterior to mid-length. Width slightly greater than length, thickness almost half the length.

Exterior of pedicle valve. Evenly convex with well-developed beak which overhangs the pedicle interarea and is almost in contact with the beak of the brachial valve. The pedicle beak projects one-tenth of total length beyond the hinge line. Lateral margins of interarea sharp.

Exterior of brachial valve. Slightly convex with a very shallow sulcus widening from the umbo to the anterior margin. Lateral margins of sulcus indefinite. Outline transversely elliptical. Cardinal angles rounded. Interarea orthocline. Notothyrium having margins which diverge only slightly, partly filled by myophore of the cardinal process which protrudes slightly. The pattern of branching of the costellae in the median area of the brachial valve is P I + P Is + P It + P I 2nd and P II + P IIs, all of which have been produced at the 5 mm. stage.

Interior of pedicle valve. A low, rounded median ridge extends from the delthyrial cavity to the centre of the valve where it ends in a gentle slope. The posterior extremity of the delthyrial cavity is flat. Adductor scars are not seen. Parallel, well impressed, narrow diductor tracks separated by the median ridge, extend to the anterior end of the ridge where they terminate with rounded margins. Low extensions of the dental lamellae bound the diductor tracks laterally. The thick vertical dental lamellae support massive teeth, whose anterior extremities are ridge-like, directed antero-laterally. The medial faces of the teeth bear deeply cut crural fossettes which are straight and inclined antero-ventrally. The posterior faces of the teeth bear accessory sockets directed antero-laterally. No pedicle callist seen.

Interior of brachial valve. Well impressed, pear-shaped adductor muscle field defined by raised margins which posteriorly fuse with the anterior edges of the brachiophore bases and anteriorly decrease towards the median ridge. In one specimen, short, low

oblique ridges extend outwards from the central part of each margin in an antero-lateral direction (see Pl. 61, fig. 18).

Muscle field equals almost two-thirds shell length and over one-third greatest width. The median ridge is narrow and rounded between anterior pair of impressions but becomes wider and flatter between posterior pair. The anterior pair is larger and sub-elliptical, posterior pair trigonal and not always clearly separated. The anterior pair well impressed. When the posterior pair is also well impressed, the transverse ridge, normal to the median ridge, emphasizes the quadripartite character.

The brachiophores are very thick, straight, erect, and proximally are separated posteriorly only by the width of the cardinal process. Distally they diverge slightly, their bases merging with the raised margin of the muscle field. In some specimens fulcral plates are visible, joining the postero-lateral surface of the brachiophore to the posterior edge of the valve and flooring the sockets which are partially excavated beneath the interarea. Sockets are large and widely divergent and sometimes crenulated. The cardinal process arises as a short shaft between the posterior edges of the brachiophores and expands to a bulbous non-lobed myophore which partially protrudes from the notothyrium.

Crenulations of the anterior shell margin are low and evenly rounded with rounded interspaces.

Holotype. GSM 102214, internal mould of brachial valve (figured Pl. 61, fig. 16). Siltstone immediately above Wenlock Limestone (? latest Wenlockian/earliest Ludlovian). Old Quarry, at Cwm, Usk inlier, Britain (Nat. Grid Ref. 33320160).

Paratypes. GSM 102207, internal mould of pedicle valve (figured Pl. 61, fig. 3). Siltstone immediately above Wenlock Limestone (? latest Wenlockian/earliest Ludlovian). Bank in field, 600 yards north-west of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825).

GSM 102216, brachial valve (figured Pl. 61, figs. 20–24) and GSM 102218, whole shell (figured Pl. 61, figs. 26–30). Wenlock Limestone (Wenlockian). Old Quarry on west side of Lincoln Hill, Iron Bridge, Britain (Nat. Grid Ref. 670038).

Distribution. This species occurs commonly in the four to six feet of buff and rust-coloured decalcified siltstones immediately overlying the Wenlock limestone in the Usk inlier. In these beds the shells have been dissolved and very clear internal and external moulds were collected, the majority being moulds of the brachial valve. Boucot collected shells, here considered to be conspecific, from the Wenlock limestone at Iron Bridge, Shrewsbury (Grid Ref. 670038 Old Quarry on west side of Lincoln Hill). So far, these are the only known occurrences of this species, the age of which is Wenlockian and possibly earliest Ludlovian. (See Walmsley, 1959, pp. 487 and 506–7 for discussion of the age of the beds at Usk).

Isorthis clivosa sp. nov.

Plate 61, figs. 31–38; Plate 62, figs. 1–22

Diagnosis. Unequally biconvex, nonsulcate to faintly sulcate with circular to transversely elliptical outline.

Median ridge of pedicle valve wide, ending in broad slope and separating narrow deeply impressed diductor tracks. Well marked vascular grooves diverge from anterior ends of diductor tracts toward anterior margin. Brachial valve has distinctly quadripartite adductor muscle field bounded by circular raised margin not extending into anterior half of valve. Median ridge narrows between larger anterior pair of impressions. Dental lamellae thick with flattened anterior edges. Brachiophores, divergent thin blades.